Mycorrhizal Hosts and Distribution of *Cenococcum graniforme*[1]

JAMES M. TRAPPE

(Pacific Northwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Portland, Oregon)

Since its original description by Sowerby in 1800, *Cenococcum graniforme* (Sow.) Ferd. & Winge (*Lycoperdon graniforme* Sow., *Cenococcum geophilum* Fr., *Mycelium radicis nigrostrigosum* Hatch) has continuously interested students of hypogeous fungi because of its singular appearance and habits. Taxonomic studies of the species, known only as a sterile mycelium, culminated in the monograph of the monotypic genus *Cenococcum* Fr. by Ferdinandsen and Winge (17). Later discovery by Lihnell (33) that *C. graniforme* formed the unique black mycorrhizae known since the 19th century (22, 34, 42) excited additional study of its ecology, distribution, and mycorrhiza formation by a sizeable number of researchers. Their reports revealed that this fungus commonly forms mycorrhizae with a broad variety of angiosperms and gymnosperms in Europe and North America.

The apparently wide adaptability of *C. graniforme* to hosts and habitats prompted me to search for its occurrence beyond areas where the fungus had previously been found. This paper presents new information on the distribution and mycorrhizal hosts of *C. graniforme* together with a compilation of previously published records to provide a summary of present knowledge.

HOSTS

Though *C. graniforme* often forms extensive mycelial systems in upper soil horizons, it has not been convincingly documented as purely saprophytic in nature; I have never found it beyond possible connection with host roots. If it is an obligate symbiont under natural conditions, the aggregate host range would delineate its potential range. Hosts forming ectotrophic mycorrhizae with *C. graniforme* reported in the literature have been summarized up to mid-1962 (55). Since then, *Pinus elliottii* (35), *P. contorta* (57), *P. ponderosa* (57), *P. cembra* (23), and several *Salix* (21) species have been added.

The families, genera, or species listed below were found by my examination of soil and root samples to have either ectotrophic or ectendotrophic mycorrhizae formed with *C. graniforme*. Names are in boldface if they are new additions, or in standard italic type if in confirmation of reports as cited previously (55)

GYMNOSPERMAE

Pinaceae

Abies alba, ***amabilis***, ***balsamea***, ***concolor***, ***grandis***, ***lasiocarpa***, ***magnifica*** vars. ***magnifica*** and ***shastensis***, ***procera***, ***sachalinensis***.
Larix decidua vars. *decidua*, *polonica*, and *sudetica*, ***laricina***, ***lyallii***, ***occidentalis***.
Picea abies, ***breweriana***, ***engelmannii***, ***glauca***, ***mariana***, ***orientalis***, ***punegns***, *sitchensis*.
Pinus ***albicaulis***, *banksiana*, *contorta*, ***coulteri***, ***echinata***, *elliottii* vars. *elliottii* and ***densa***, ***glabra***, ***jeffreyi***, ***koraiensis***, ***lambertiana***, ***massoniana***, ***monophylla***, ***monticola***, *mugo*, *nigra* var. *poiretiana*, ***palustris***, ***pinaster***, ***pinea***, *ponderosa*, ***radiata***, *resinosa*, ***serotina***, *strobus*, *sylvestris*, *taeda*, *virginiana*.
Pseudotsuga ***macrocarpa***, *menziesii* vars. ***glauca*** and *menziesii*.
Tsuga canadensis, ***heterophylla***, ***mertensiana***.

ANGIOSPERMAE

Betulaceae

Alnus ***crispa***, ***rubra***, ***rugosa***, ***sinuata***, ***tenuifolia***.
Betula ***fontinalis***, ***lenta***, ***lutea***, ***nigra***, ***occidentalis***, ***papyrifera***, ***platyphylla*** var. ***japonica***, ***pumila***.
Carpinus betulus, ***caroliniana***.
Corylus cornuta vars. ***californica*** and *cornuta*.

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Ericaceae
Arctostaphylos uva-ursi.
Fagaceae
Castanea dentata, sativa.
Castanopsis chrysophylla, sempervirens.
Fagus grandifolia, multinervis, orientalis, sylvatica.
Lithocarpus densiflorus.
Nothofagus antarctica, pumilio.
Quercus agrifolia, alba, borealis, breweri, chrysolepis, falcata, garryana, kelloggii, laevis, macrocarpa, ×moreha, oblongifolia, petraea, prinus, robur, sadleriana, vaccinifolia, virginiana.
Myrtaceae
Eucalyptus gigantea.
Rosaceae
Cercocarpus ledifolius.
Chamaebatia foliolosa.
Rosa gymnocarpa.
Sorbus sitchensis.
Salicaceae
Populus angustifolia, balsamifera, deltoides, tremuloides, trichocarpa.
Salix babylonica, bebbiana, bella, coulteri, geyeriana, hookeriana, humilis, lasiandra, lutea, petrophila, piperi, scouleriana.
Tiliaceae
Tilia americana, cordata, europaea.

In one or more habitats, all species of Pinaceae, Betulaceae, Fagaceae, and Salicaceae that I have examined possess mycorrhizae formed by *C. graniforme*. Apparently, the fungus can form mycorrhizae with all members of these families if conditions are suitable. Not enough is known about the mycorrhiza-forming proclivities of genera in the other families listed to speculate on their breadth of association with *C. graniforme*. For example, renantherous species of eucalypts are known to possess ectotrophic mycorrhizae (46), but until now *C. graniforme* had never been reported on eucalypt roots.

Ericaceous species do not usually form characteristic ectotrophic mycorrhizae, but *Arctostaphylos uva-ursi* is one exception (7, 45). *C. graniforme* is frequently its mycorrhizal associate in Oregon and Washington.

The unusual symbiotic ability of *C. graniforme* is emphasized by its occasional formation of ectotrophic mycorrhizae with species that normally form only endotrophic mycorrhizae: *Juniperus communis* in Cupressaceae (32), *Acer pseudoplatanus* in Aceraceae (15, 16), *Lactuca muralis* in Compositae (5), *Vicia sylvatica* in Leguminosae (8), *Galium schultesii* and *G. rotundifolium* in Rubiaceae (16), and *Dryopteris filixmas* in Polypodiaceae (16). Equally unusual is an endotrophic mycorrhiza formed by *C. graniforme* with *Stellaria holostea* in Caryophyllaceae (8).

DISTRIBUTION

The known range of *C. graniforme* has been delineated from personal observation and reports in the more important literature. The summary of Ferdinandsen and Winge (17) is cited for most pre-1925 reports of distribution. References which did not name the fungus specifically but described or illustrated it sufficiently for positive identification are asterisked. Representative locations have been selected from my identifications to illustrate extensions of previously known range. Locations are given by names of nearby geographic features. Where named features were not nearby, latitudes and longitudes are listed. Specimens deposited in the University of Washington Mycological Herbarium are denoted by my collection numbers in parentheses.

NORTH AMERICA
CANADA
ALBERTA
Jasper, 1,070 m
BRITISH COLUMBIA
Mount Revelstoke, 1,980 m
Kaslo, 550 m
Kelsey Bay, Vancouver Island, 15 m
MANITOBA
Whitemouth Lake, 370 m (Trappe#17)
NEWFOUNDLAND
Avalon Peninsula, 120 m (Trappe #16)
NORTHWEST TERRITORIES
Fort Simpson, 120 m (Trappe #14)
SASKATCHEWAN
Christopher Lake, 330 m (Trappe #15)
YUKON TERRITORY
Haines Junction, 600 m (Trappe #40)
UNITED STATES
ALASKA
Firth River, 68°45'N lat, 141°0'W long, 610 m at northern limit of *Picea glauca* (Trappe #13)
Kotzebue Sound, 8 m, on *Salix* sp. in tundra
Chandler River, 67°N lat, 147°W long, 270 m
Washington River, 65°N lat, 142°W long, 490 m
Ladue River, 63°N lat, 142°W long, 910 m
Purgatory, 66°N lat, 148°W long, 300 m
Northway, 63°N lat, 142°W long, 530 m
Kenai, 61°N lat, 151°W long, 45 m
Admiralty Island, 230 m (Trappe #12)
Sitka, Baranof Island, 50 m (Trappe #9)
Nakwisne Bay, Baranof Island, 40 m (Trappe #8)
Duncan Canal, Kupreanof Island, 30 m (Trappe #10)
Hollis, Prince of Wales Island, 240 m (Trappe #11)
ARIZONA
Fort Valley, 2,290 m
Madern Canyon, Santa Rita Mountains, 1,830 m
ARKANSAS
Crossett, 55 m
CALIFORNIA
Lassen National Park, 1,615 m
Mineral, 1,620 m
South Fork of American River, 975 m
Monterey, 240 m
Lake Arrowhead, 2,000 m (Trappe #101)
COLORADO
Front Range, 40°N lat, 106°W long, 2,740 m
FLORIDA
Osceola National Forest, 30°N lat, 92°W long, 45 m
Corkscrew Experimental Forest, 26°N lat, 82°W long, 8 m
GEORGIA
Wayne County, 31°N lat, 82°W long, 30 m
Pierce County, flood plain of Santilla River, 10 m
Charlton County, 31°N lat, 82°W long, 30 m
IDAHO
Bonners Ferry, 550 m
Idaho City, 1,220 m
INDIANA
Paoli, 240 m
KENTUCKY
Baldrock Experimental Forest, 37°N lat, 84°W long, 400 m
LOUISIANA
Alexandria, 35 m
MAINE
Bradley, 40 m
MARYLAND
(25)
MASSACHUSETTS
Hopkins Experimental Forest, 42°N lat, 73°W long, 305 m
MICHIGAN
Calhoun County, 43°N lat, 90°W long, 250 m
MINNESOTA
Itasca County, 47°N lat, 94°W long, 400 m
MISSISSIPPI
Benoit, 30 m
Vicksburg, 90 m
MISSOURI
Dent County, 38°N lat, 91°W long, 90 m
MONTANA
Kiowa, 1,370 m
Hegben Lake, 2,040 m
NEVADA
Dog Valley, 39°N lat, 120°W long, 1,770 m
NEW JERSEY
(17, 27)
NEW YORK
(27)
NORTH CAROLINA
(14)
NORTH DAKOTA
Turtle Mountain, 670 m
ORGEON
Sand Lake, 6 m
Aloha, 120 m
Timberline Lodge, Mount Hood, 1,980 m
Starkey, Blue Mountains, 1,680 m
Francis Lake, Wallowa Mountains, 2,290 m
Mount Scott, Crater Lake National Park, 2,680 m
McKenzie Pass, 1,620 m (Trappe #18)
Fort Rock, 1,520 m
Brookings, 20 m
Bandon, 20 m
Siskiyou Mountains, 43°N lat, 123°W long, 910 m
PENNSYLVANIA
Irving, 365 m
SOUTH CAROLINA
Francis Marion National Forest, 33°N lat, 80°W long, 30 m

SOUTH DAKOTA
Black Hills, 45°N lat, 103°W long, 1,710 m
VERMONT
Jerico, 180 m
VIRGINIA
Charlottesville, 170 m
Chatham, 210 m
WASHINGTON
Whidbey Island, 45 m
North Star Mountain, Chelan County, 2,410 m
Sprague, 610 m
Tonasket, 270 m
Leahy, 390 m
Metaline Falls, 630 m
Spokane, 590 m
Yakima Park, Mount Rainier, 2,440 m
Hoquiam, 60 m
Forks, 60 m
Wind River Experimental Forest, 46°N lat, 122°W long, 760 m
WISCONSIN
(40)

SOUTH AMERICA
ARGENTINA
TIERRA DEL FUEGO
Valle del glacier Martial, Ushuaia, 280 and 330 m (Trappe #3 and #4)
CHILE
MAGALLANES
Monte Alto, Puerto Natales, 250 m (Trappe #5)

EUROPE
AUSTRIA (23)
BELGIUM (17, 31)
CZECHOSLOVAKIA (17, 48*, 53*)
DENMARK (17, 33, 42*, and others)
FINLAND (17, 39, 41, 52, and others)
FRANCE (4, 13, 17, 34*, and others)
GERMANY (17, 28, 29, 30, 38, 56, and others)
GREAT BRITAIN AND IRELAND (17, 26, 47, and others)
ITALY (17, 20, 21, 22*)
NETHERLANDS (43)
NORWAY (17)
POLAND (5, 8, 9, 10, 11, 12, 14, 15, 16, 44, and many others)
PORTUGAL (18, 19, and others)
SOVIET UNION (1*, 6*, 17, 24, 50, 51, and others)
SWEDEN (2, 3, 17, 32, 33, 37*, 39, 49, and others)
TURKEY
Istanbul, Belgrad Forest, 110 m (Trappe #6)

AFRICA
UNION OF SOUTH AFRICA
Stellenbosch, 410 m (Trappe #1)
MOROCCO
Larache Nursery, 10 m
Ifrane, 1,600 m

ASIA
HONG KONG
50 m (Trappe #102)
KOREA
Suwon, Kwang-noong Experimental Forest, 200 m (Trappe #7)
JAPAN (36*)
INDIA
Dehra Dun, New Forest, 700 m

AUSTRALIA
Near Canberra City, 1,200 m (Trappe #2)

The distribution of *C. graniforme* (fig. 1) as generalized from locations listed above suggests substantial discontinuities in its occurrence. Within host ranges north of 30° N lat, however, it has usually been found where sought. Moreover, its ability to grow from hot, semiarid to arctic-alpine environments is well known (e.g., 8, 12, 39, and 54). In all likelihood, many blank spaces on the map north of the tropics will be eliminated as additional collections are made.

How common *C. graniforme* may be in the Southern Hemisphere remains unknown at present. First reports of its occurrence south of the equator, as given in this paper, are too scanty to suggest its possible distribution. Collections from South Africa, provided by Mr. D. G. M. Donald, were from plantations of exotics—*Quercus robur*, *Salix babylonica*, and *Pinus pinea*. It is possible that *C. graniforme* was imported with planting stock (the oak was planted some 150 years ago; the pine, 100 years ago). In contrast *C. graniforme* was found on indigenous hosts in Argentina and Chile (*Nothofagus antarctica* and *N. pumilio*, collected by Dr. E. Horak) as well as in Australia (*Eucalyptus gigantea*, collected by Mr. Graham Chilvers).

Distribution of *C. graniforme* in tropical latitudes is problematical. A single collection from Hong Kong contained a few small sclerotia and hyphal fragments. My examination of pine root samples from Puerto Rico revealed one dead mycorrhiza formed with *C. graniforme* out of many hundreds formed by other fungi. The fragments of attached hyphae were too few to provide suitable herbarium material. No typical sclerotia were found. In this case, the fungus could well have been imported with humus brought to Puerto Rico from southeastern United

States. A total of 35 samples from Hawaii and tropical Brazil, including both exotic pines and native species, were devoid of *C. graniforme*. Since *C. graniforme* commonly grows in temperate to alpine climatic zones where suitable hosts are available, it may extend more or less continuously through the tropical latitudes at higher elevations in the North and South American cordilleras.

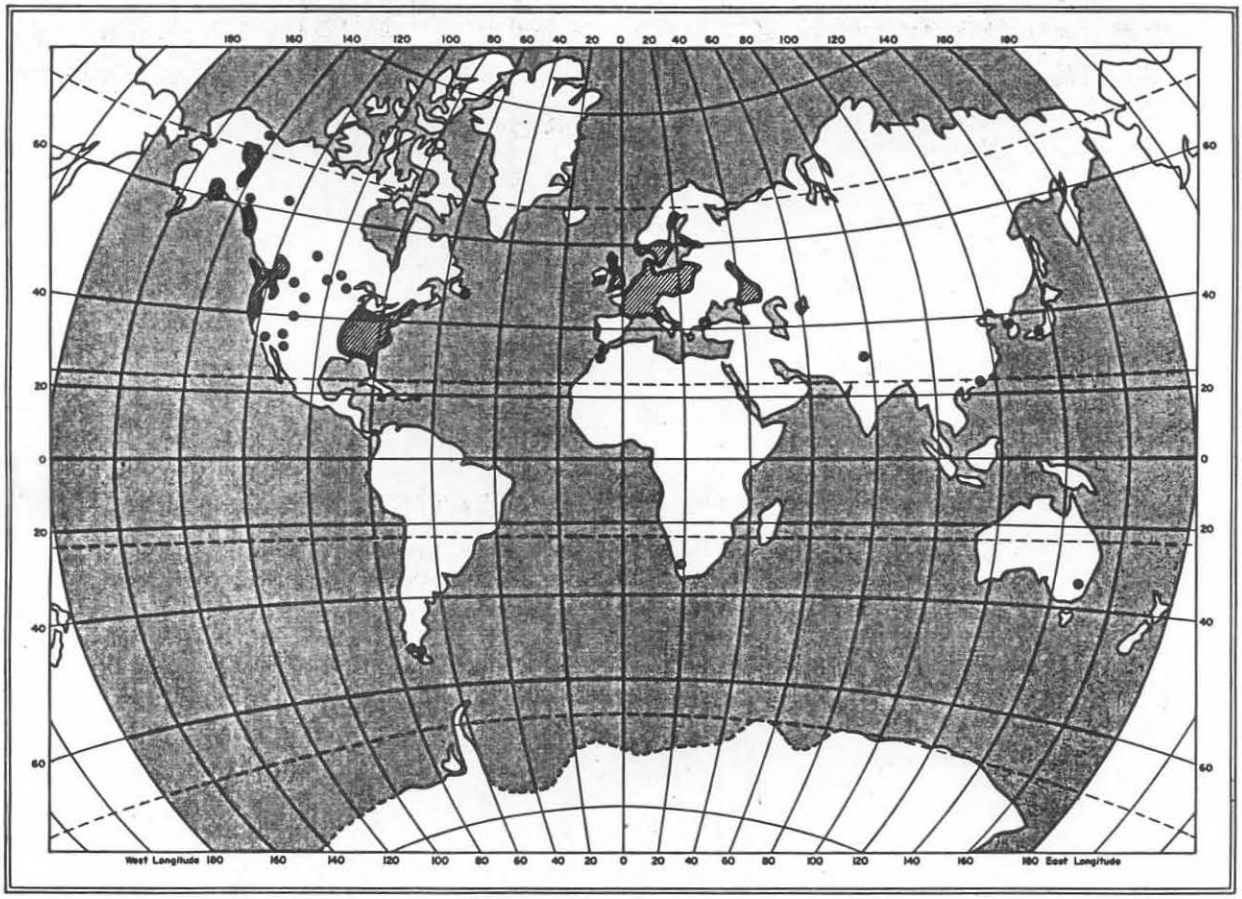

FIG. 1. *Generalized distribution of Cenococcum graniforme. Shading encompasses areas in which it is known to be broadly distributed. Spots indicate single collections.*

SUMMARY

Many new mycorrhizal hosts for *Cenococcum graniforme* (Sow.) Ferd. & Winge are added to those previously reported. The large number of known hosts emphasizes the wide adaptability of this fungus and suggests that it can probably form ectotrophic mycorrhizae on most ecto-mycotrophic hosts. Its hitherto unknown presence in the Southern Hemisphere plus new localities in the Northern Hemisphere are also reported. Because *C. graniforme* can grow in a striking variety of habitats, there seems strong likelihood that it will ultimately be found to occur throughout the world where temperate to arctic-alpine climates prevail and suitable hosts are present.

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